

**BEHAVIOR OF SADDLED PROMINENT
HETEROCAMPA GUTTIVITTA (WALKER)
(LEPIDOPTERA: NOTODONTIDAE) LARVAE
IN THE NORTHERN HARDWOOD FOREST**

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Abstract.—Feeding and movement of saddled prominent, *Heterocampa guttivitta* Walker (Lepidoptera: Notodontidae) caterpillars were investigated in a northern hardwood forest in upstate New York. The insect is a midseason defoliator. Growth and feeding occur during the warmest and most stable period of year with respect to weather. Weather did not detectably affect feeding or movement behavior. However, total foliage consumption and consumption rate were related to temperature (as determined in the laboratory). The rate of movement between feeding sites increased with older instars. Both feeding and movement exhibited a diel cycle: feeding was greatest during the night, and movement was greatest during the day. Observations are discussed in terms of three currently popular hypotheses explaining caterpillar behavior: that their movement and feeding patterns are a response to weather conditions, variable and unpredictable food quality, or vertebrate predation.

The saddled prominent, *Heterocampa guttivitta* (Walker), (Lepidoptera: Notodontidae) is a periodic defoliator of northern hardwood forests where American beech, *Fagus grandifolia* Ehrh., sugar maple, *Acer saccharum* Marsh., and yellow birch, *Betula alleghaniensis* Britton are principle constituents. During outbreaks, these three species are consistently the most severely defoliated. Species of *Quercus*, *Populus*, *Prunus*, *Hamamelis*, as well as other *Betula* are defoliated to a lesser degree, suggesting that saddled prominent is capable of broad polyphagy. Defoliation reports of some plant species conflict (e.g., *Acer rubrum* L., *Populus deltoides* Bartr. ex Marsh.); however, *Fraxinus* sp., *Tilia* sp. and *Acer pennsylvanicum* L. are clearly unsuitable hosts (Patch, 1908; Martinat, 1984). Outbreaks have occurred in northeastern United States and southeastern Canada every eight to twelve years since 1907. The last major outbreak occurred in eastern Maine where 405,000 hectares were defoliated in 1977 (Martinat and Allen, 1988).

The saddled prominent is indigenous and occurs throughout eastern United States and southeastern Canada. Its seasonal history is well known only in upstate New York and New England (Allen and Grimble, 1970; Martinat, 1984). Here it is univoltine, overwinters as a pupa, and emerges from late May to late June. Eggs are laid singly on the foliage of host tree species selected by the free-flying female. Eggs eclose

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in 9–10 days. First instars skeletonize the lower epidermis of leaves. Later instars feed from leaf margins inward, leaving irregularly shaped uneaten portions. Caterpillars cease feeding 24–48 hours prior to moulting, and remain quiescent on the undersurface of foliage on a silk mat. There are five larval instars, and peak defoliation occurs from mid-July through early August. The period of egg development, eclosion, and caterpillar feeding is therefore approximately early June through early August. Mature caterpillars drop from the foliage or descend tree boles, burrow into the litter below the host tree, and form a loose pupal cell of silk and litter particles. Pupation occurs following a two to three day prepupal period. By mid-August, most caterpillars have pupated.

In an attempt to more clearly understand saddled prominent outbreak dynamics, Martinat and Allen investigated the spatial and temporal aspects of outbreaks (1988), the relationship between outbreaks and drought (1987a), and caterpillar development and survivorship in the laboratory (1987b). Although caterpillar biology and fitness in the laboratory are clearly affected by temperature and humidity, we wished to determine actual conditions experienced by larvae in the forest, and determine if their behavior is affected by changing weather conditions. We therefore studied unconfined caterpillars in their natural habitat, a northern hardwood stand. We report here the results of these observations.

MATERIALS AND METHODS

Studies were conducted from May through August in 1978, 1979, and 1980 at the New York State Ranger School, Wanakena (St. Lawrence County), in an approximately 80-year old stand of pole-sized (12.5–30 cm diameter at breast height) sugar maple and beech. A Foxboro hygrothermograph and Taylor barograph were maintained at the study site. Charts were changed and the hygrothermograph calibrated with sling psychrometer and max/min thermometer weekly from May through September.

Feeding activity and movement. Several hundred first and second instars and eggs were gathered from sugar maple at the beginning of the feeding season and placed on the foliage of several closely spaced sugar maple trees (approximately two per 1-meter branch section, to avoid crowding). Scaffolding with platforms at two and four meters above the ground was placed around the foliage to facilitate close observation. The activity of individual caterpillars was monitored over three to four day periods throughout the season by tagging leaves on which caterpillars were found. They were observed day and night at four to six hour intervals. An observation consisted of recording instar and activity of each caterpillar, approximate portion of leaf eaten since last observed (sketched over outlines on the data sheets), and leaf exposure to sun (in direct sun or shaded). At the time of observation, temperature, barometric pressure, relative humidity (converted to saturation deficit prior to analysis), percent cloudiness, and precipitation (none, light, heavy) were recorded. Individuals which disappeared for unknown reasons between observations were deleted from the data set prior to analysis.

Four to six observations were made within each 24-hour period. Observations continued throughout the summer until larvae completed feeding and vacated the foliage. For analysis, observations were summarized as categorical data per individual (feeding vs. not feeding, moved vs. not moved since last observation, moved within

the same leaf cluster vs. moved to a different cluster, etc.). Data were then compiled into frequency tables and χ^2 tests applied.

Moulting requires one to two days during which the caterpillar remains quiescent and attached to a silken mat on the undersurface of a leaf. A caterpillar found in this condition was assumed to be incapable of feeding or movement, and was therefore subtracted from the total number in the observation.

Foliage consumption. Records of foliage consumption were kept for larvae reared in the laboratory in 8 oz. cups on fresh sugar maple foliage. Approximately 100 individuals were randomly assigned to one of three environmental chambers, the temperature cycles of which were set to simulate the difference in temperature between day (06:00–18:00 hr) and night (18:00–06:00 hr): cycle A, 12.8°C night, 23.9°C day; cycle B, 15.6°C night, 26.7°C day; and cycle C, 18.3°C night, 29.4°C day. Automatic cams on the timing mechanisms of the environmental chambers were cut so that the 5.6°C change occurred gradually over four hours. Fresh sugar maple leaves were photocopied before and after each period of larval feeding, and the amount of foliage consumed was determined to the nearest 0.01² inch using a dot grid to measure the amount of foliage removed.

RESULTS

Caterpillar feeding and foliage consumption. Larval development rate is affected by both temperature and humidity (Martinat and Allen, 1987b). Foliage consumption rate is also affected by temperature (Fig. 1). The relationship is most evident during the last two stadia, where about 85% of all consumption occurs.

In the two years of this study, we found few weather conditions in which feeding was not observed. The number of larvae observed feeding was not detectably affected by changing temperature, humidity, barometric pressure, or cloudiness. Larvae were observed feeding in light and moderate rain. Only during intense thunderstorms, which typically lasted no more than 20 minutes, did all feeding apparently stop.

Feeding in all instars exhibited a diel rhythm: greater numbers of larvae were observed feeding at night (19:00–06:00 hours) than during the day (07:00–18:00 hours) (Fig. 2). It is therefore interesting to note that, although consumption rate is temperature dependent, feeding as an activity is apparently not, at least within the range of temperatures observed in the forest during this study. Indeed, feeding activity was greatest during the night when temperatures are typically lowest.

Caterpillar movement. First instars rarely left the leaf on which they eclosed. Later instars moved frequently whether or not the leaf on which they fed was completely consumed. Second and third instars rarely consumed an entire leaf prior to moving, but fourth and fifth instars were sometimes forced to move in response to depletion of local foliage (Fig. 3). Therefore, the frequency of movement increased with caterpillar age. During the day, 65% (N = 134) of fifth instars, 45% (N = 84) of fourth instars, and 35% (N = 73) of second and third instars had moved after six hours, on the average. Movement activity was greater during the day than during the night (Fig. 2). Approximately 80% of all movement by all instars was to a new leaf cluster or branch, indicating that caterpillars frequently bypass local food sources. However, this was also related to instar. Older caterpillars more frequently moved to a distant leaf cluster rather than from one leaf to another in the same cluster (Fig. 4). Fourth

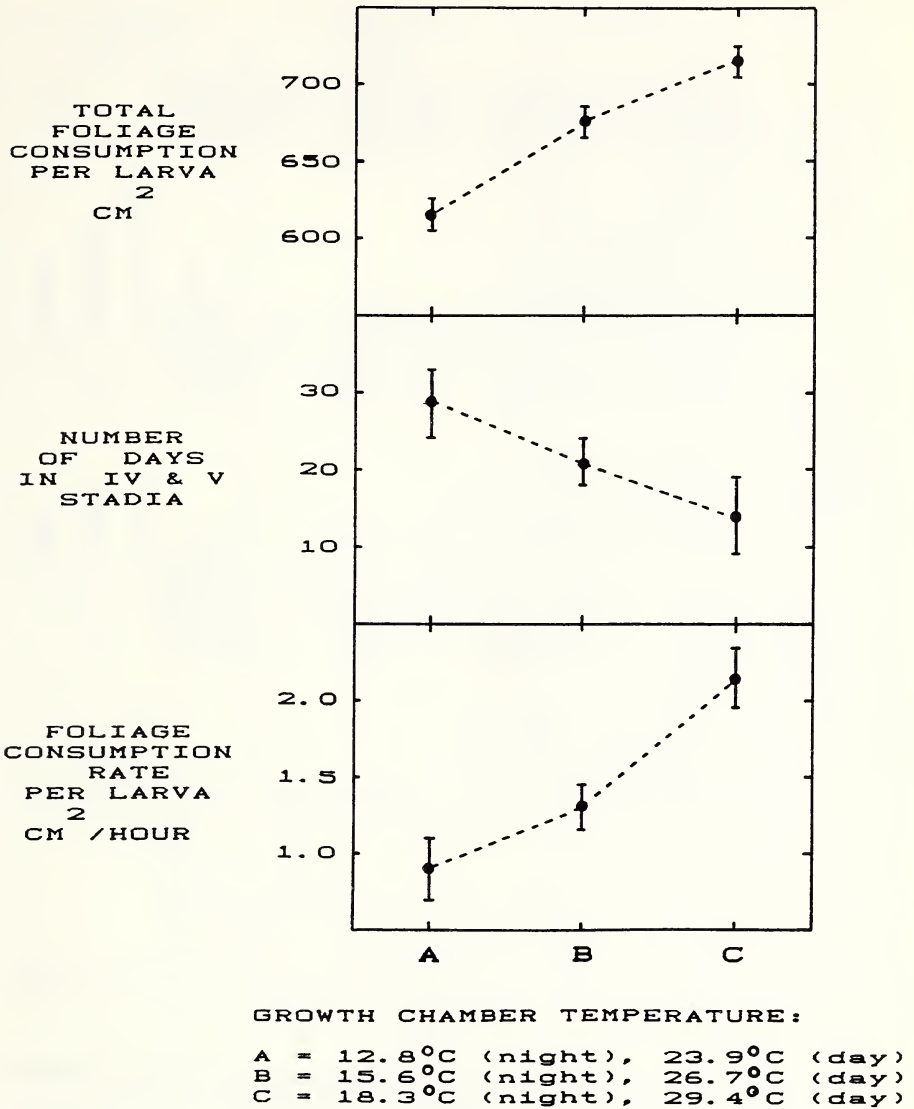


Fig. 1. Foliage consumption of fourth and fifth instars reared under three different temperature cycles. A statistical test (Student-Newman-Keuls procedure, Sokal and Rohlf, 1981) showed that differences in foliage consumption between all three temperature cycles (top graph) were significant ($P < 0.05$).

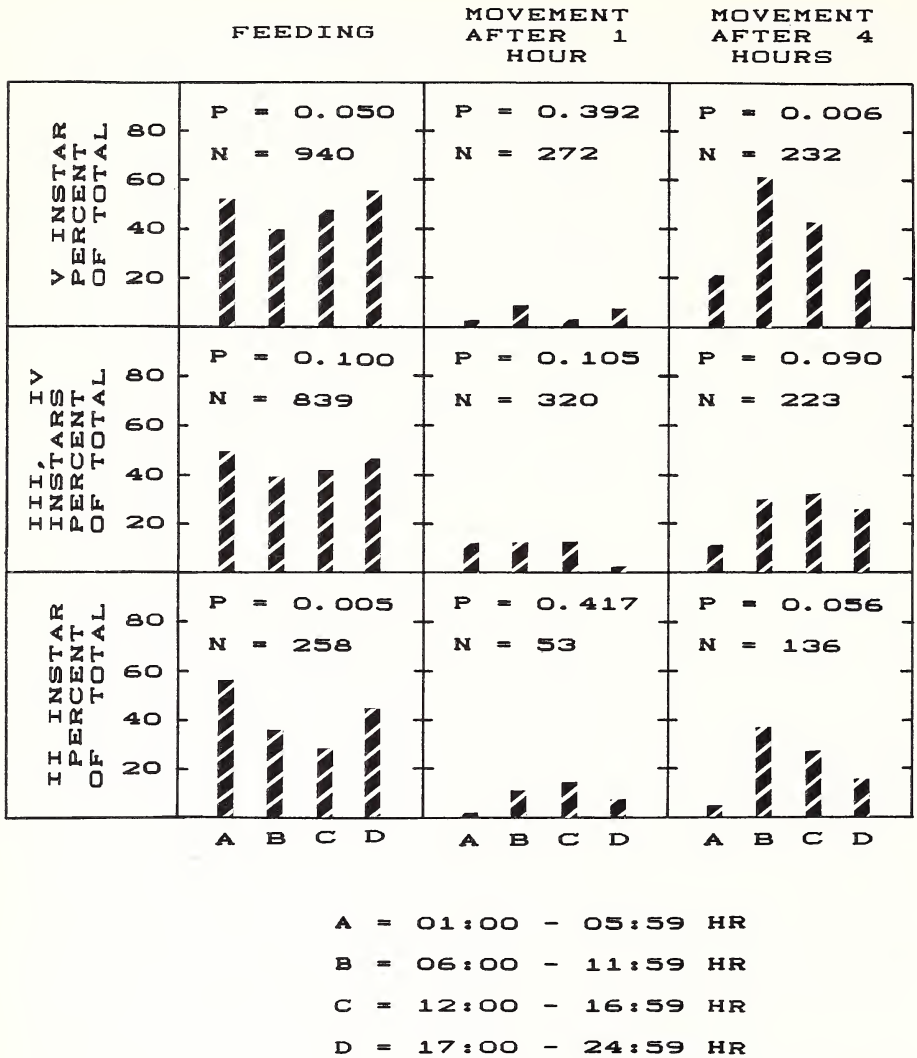


Fig. 2. Caterpillar diel feeding and movement activity, by instar. Probabilities are those of the χ^2 test statistics obtained in tests of independence (Sokal and Rohlf, 1981).

and fifth instars generally moved longer distances to reach new feeding sites than did earlier instars.

DISCUSSION

In the northern hardwood forest, saddled prominent caterpillar development and feeding occur during the warmest and most stable period of year with respect to weather. During this period, nocturnal temperature minima may occasionally drop

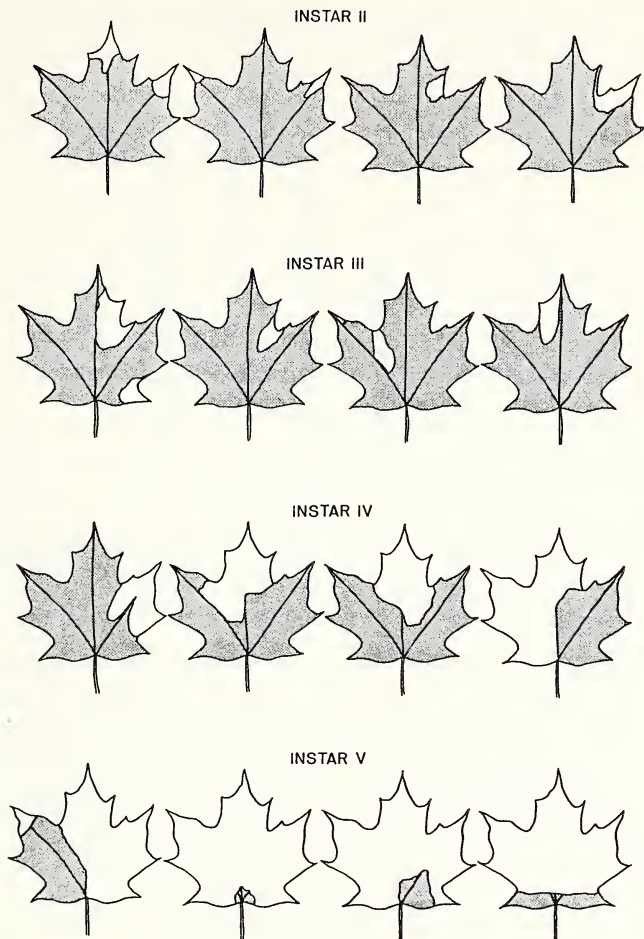


Fig. 3. Sugar maple leaf portions left by saddled prominent caterpillars after they abandoned the leaf in search of another. Leaves of approximately the same size were chosen for illustration.

to 10°C or lower (the temperature at which feeding and movement ceases, Martinat and Allen, 1987b), but caterpillars are exposed to this extreme for no more than a few hours on a given night, at the most. High temperatures or direct solar radiation can also affect caterpillar behavior (Sherman and Watt, 1973; Casey, 1977), but this is also unlikely in our study. Individuals were situated far below the canopy, and thus well shaded. In addition, the average maximum daytime temperature during the hottest two weeks of the summer (16–31 July) was 25.7°C; well below the temperature causing high physiological stress and reduction in development rate or death (T_m , Martinat and Allen, 1987b). Therefore, interruption of feeding due to severe weather conditions is probably rare for saddled prominent larvae.

Early season defoliators are likely to be subject to inclement weather. For example,

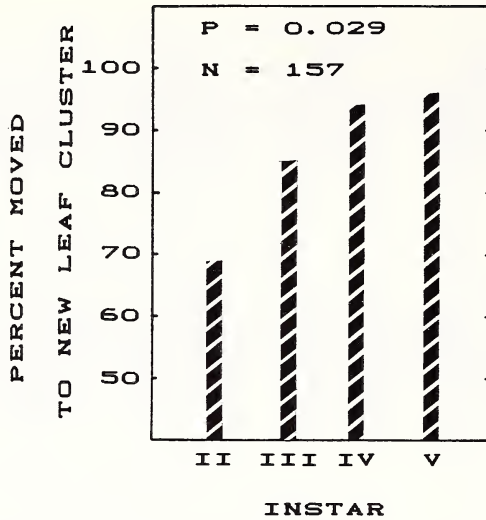


Fig. 4. Percent caterpillars that moved to a new leaf cluster versus the alternative: moved to a new leaf in the same cluster, by instar. Observations were four hours apart. Probability is that of the χ^2 test statistic obtained in a test of independence (Sokal and Rohlf, 1981).

an unusually warm early spring followed by a late spring frost can devastate a forest tent caterpillar (*Malacosoma disstria* Hbn.) population (Blais et al., 1955). In addition, a greater contrast between day and night conditions and a greater frequency of frontal weather increases the unpredictability of daily ambient conditions and reduces the time available for feeding (Wellington, 1954). Similar problems are probably faced by late season defoliators (Morris, 1964, 1967; Morris and Bennett, 1967). A midseason defoliator, however, is less likely to be exposed to inclement conditions. We found this to be the case in our study. We conclude that weather is not the principle cause of caterpillar feeding and movement patterns.

Nevertheless, late instar saddled prominent caterpillars are active wanderers, even in low density populations such as in our study. During the day, they usually remain on a leaf less than eight hours whether or not the leaf is consumed. They often travel several meters to a new cluster and bypass many potential feeding sites. Two alternative hypotheses explaining caterpillar behavior are current in the literature; first, that movement and feeding are a search for optimal but unpredictable food quality (Schultz, 1983); or second, that they are part of a vertebrate predator avoidance strategy (Heinrich, 1979, 1983). Neither of these alternatives alone is a satisfactory explanation of our observations.

Schultz observed that saddled prominent caterpillars accepted only 31% of encountered leaves for sustained feeding, and called them "choosy feeders." Our observations generally concur with Schultz. However, if his interpretation is correct, then not all instars are equally choosy. First instars do not move from the leaf on which they eclose. They do not disperse in the manner of first instar gypsy moths, for example. Initial food plant selection is accomplished by the female when she oviposits. Therefore, first instars must accept the foliage on which they eclose what-

ever its nutritional value, or starve. It may be too energetically costly or hazardous for a first instar to wander in search of food. The high mortality among first instars (Martinat and Allen, 1987b) may then be due to forced acceptance of nutritionally poor foliage. Induction of detoxification systems may occur less readily in early instars (Gould and Hodgson, 1980), and they may be less tolerant of poor food quality (Chan et al., 1978). If first instars survive on less than optimal foliage, the cost may appear as reduced adult fitness.

Heinrich (1979) interpreted a number of saddled prominent behavioral traits as defensive strategies against visually cued vertebrate predators: preference for night feeding, "trimming" leaves rather than leaving leaf shreds, clipping off uneaten portions of leaf by chewing through the petioles (thus removing leaf damage which predaceous birds might use as a cue), and moving away from feeding sites and hiding after bouts of feeding. Except for preference for night feeding, we did not observe these behaviors in our study. In high density populations the forest floor is littered with leaf fragments, but we did not observe "trimming" or "clipping," nor any consistent pattern with regard to which part of a leaf was eaten or what was done with the remainder. Movement was highest during the day and was not away from, but between feeding sites. Caterpillars remained exposed and quite visible throughout the day on twigs and branches as well as foliage.

Although we took no data on predation rates, predation by invertebrates such as foliage inhabiting spiders and *Podisus* sp. (Hemiptera: Pentatomidae) was frequently observed. This casual observation suggests to us that caterpillar movement might just as easily be interpreted as a defensive strategy against invertebrate as against vertebrate predators.

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